



***Lobithelphusa mexicana* Rodriguez, 1982 (Decapoda: Pseudothelphusidae): a reassessment of key characters and systematics**

JOSÉ LUIS VILLALOBOS-HIRIART^{1,5}, SEYIT A. KAMANLI^{2,3,4},
FERNANDO ÁLVAREZ¹, AMIN GARBOU³ & PAUL F. CLARK²

¹*Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, Ciudad de México, 04510, México*

²*Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, England*

³*Imaging and Analysis Centre, Core Research Laboratories, The Natural History Museum, Cromwell Road, London, SW7 5BD, England*

⁴*Department of Biology, Faculty of Art and Science, Burdur Mehmet Akif Ersoy University, Burdur 15030 Turkey*

⁵*Corresponding author. E-mail: hiriart@unam.mx*

Abstract

Lobithelphusa Rodriguez, 1982 is endemic to southern Mexico. Assigned to this monotypic genus is the freshwater pseudothelphusid crab, *L. mexicana* Rodriguez, 1982. The original description based on an old, dry, male specimen in the collections of the Natural History Museum, London, is brief and the crab was only partially figured. *Lobithelphusa mexicana* has subsequently never been recorded from Mexico and, consequently, the conservation status of this species is unknown. The type specimen has a complete, but detached left chela; is devoid of the left ambulatory pereopods 1–3, with the fourth missing the carpus, propodus and dactylus; and its left first gonopod detached but retained in a glass tube kept adjacent to the crab. In spite of this damage the crab is still in remarkably good condition for a specimen registered in 1860. The purpose of this study is to apply computed tomography (CT) scanning techniques on the extant type, including its first gonopod, in order to provide detailed illustrations of the crab. These, in turn, shall be used to re-describe the species in order to help establish the current distribution status of *L. mexicana* in Mexico, and clarify its systematic position within the Pseudothelphusidae Ortmann, 1893.

Key words: Micro-CT scanning, Hypolobocerini, Mexico, *Lobithelphusa mexicana* redescription, male gonopod morphology

Introduction

The crabs of the family Pseudothelphusidae Ortmann, 1893, are an important group of the invertebrate freshwater fauna of Mexico, Central and South America, currently comprising 309 species assigned to 49 genera, which is a significant increase from the 278 species (41 genera) reported by Villalobos-Hiriart & Álvarez (2008) and Yeo *et al.* (2008). In Mexico, pseudothelphusids are a highly diversified group of aquatic crustaceans represented by three tribes, 16 genera and 66 species (Table 1). The Pseudothelphusini Ortmann, 1897, are dispersed across central, western and northwestern Mexico, with five genera and 39 species (Villalobos-Hiriart 2005; Villalobos-Hiriart & Álvarez 2008; Villalobos & Alvarez 2010; Ojeda-Escoto *et al.* 2017); the Potamocarcinini Ortmann, 1897, are recorded from southern Mexico (mainly from the Isthmus of Tehuantepec to southern Chiapas), and Central America to northwestern Colombia, comprising 9 genera and 24 species; and members of Hypolobocerini Pretzmann, 1971, which include *Lobithelphusa* and *Spirothelphusa* Pretzmann, 1965, with 1 species each (Villalobos-Hiriart & Álvarez 2008). The other 9 genera of Hypolobocerini are distributed throughout Central and South America (Pretzmann 1972; Rodriguez 1982; Campos 2005; Campos & Magalhães 2014).

The male holotype of *L. mexicana* in the dry collection of the Natural History Museum, London (NHMUK), was collected ca. 160 years ago and represents the northernmost record for Hypolobocerini. This specimen has a

complete, but detached, left chela, is devoid of the left ambulatory pereopods 1–3, with the fourth ambulatory leg missing the carpus, propodus, and dactylus; and its left first gonopod (G1), has been removed, but is retained in a glass tube adjacent to the crab. Although damaged and registered in 1860, this specimen is however, still in a remarkably good condition.

The purpose of the present study was to apply micro-computed tomography (CT) scanning techniques on the type specimen, supplement the original morphological description with additional characters and elaborate on the figures of the carapace, chelae, and G1. Furthermore, on the basis of the G1 morphology presented here, the systematic position of *Lobithelphusa* within the Hypolobocerini is assessed and discussed.

Material and methods

The dry specimen of *Lobithelphusa mexicana* Rodriguez, 1982, was visualised using a Nikon Metrology HMX ST 225 micro-CT scanner. The whole crab and the separated chela were scanned at 150 kV (kilovolt) and 160 μ A (microamperes), while the first gonopod was scanned at 140 kV and 160 μ A. A total of 3143 X-ray projections were taken over 360° rotation in order to create the images produced for this study. The whole specimen and the chela were placed onto a polystyrene foam board, whereas the small gonopod was placed into a cut-down plastic pipette and the gaps were filled with cotton in order to hold it steady during the micro-CT scanning process.

VGStudio Max (version 2.2) was initially used to view the samples immediately after the scanning by converting the data into TIFF stack formats in order to process the data using the open source 3D surface rendering program Drishti (Limaye 2012). The stack data stored as TIFF images were then imported using Drishti import (Ball *et al.* 2017; Kamanli *et al.* 2017; Koch *et al.* 2017) and processed using Drishti. The most suitable positions of the images were taken as snapshots at different angles and saved in JPEG format. Adobe Photoshop (version CS5) was applied to final images to adjust subject brightness and contrast, to remove imaging artefacts and saved at 600 dpi in TIFF format.

The data was also converted into video format after processing the data using Drishti. In order to make the videos, after applying all the defined processes, the command of “addrotationanimation” was commenced by depressing “spacebar” on keyboard. When the “Command Help” box appeared, “addrotationanimation \times 360” command was typed in Command String Box and OK was clicked. This applied a 360° rotation in the x axis. Conversely, if rotation in the “y” or “z” axis was required then “addrotationanimation y (z) 360”! was chosen. After converting the confocal data following the specific instructions into Drishti format, the video can be created as a final step (Koch *et al.* 2017). The videos are available as Supplementary Material here.

Terminology for the morphology of the first gonopod follows Smalley (1964a), Rodriguez (1982), and Villalobos-Hiriart (2005). G1 is the abbreviation for male first gonopod.

Taxonomy

Family Pseudothelphusidae Ortmann, 1893

Subfamily Pseudothelphusinae Ortmann, 1893

Tribe Hypolobocerini Pretzmann, 1971

Genus *Lobithelphusa* Rodriguez, 1982

Diagnosis. Carapace with flat dorsal surface, regions distinct, median groove shallow, lateral margin granulated (Fig. 1a). Third maxilliped with merus of endopod subrectangular, wider than long, anterior border straight, lateral border slightly rounded; ischium trapezoidal, distal half widening; length of exopod half that of ischium (Fig. 1b–d). Male G1 of uniform thickness along its length, caudo-cephalically compressed; distal elements well developed. In mesial view (Fig. 2a), mesial surface ending distally in prominent, spinulose distal lobe (mdl) and a subdistal acute, triangular spine (mssp), cephalomesially directed. Oval gap (og) forming between distal lobe and subdistal spine. In lateral view (Fig. 2b), surface of gonopod smooth, middle portion slightly constricted and standing out as

wide, rounded rib; distal half punctate, ending apically in shoulder (lsh) next to rounded lateral crest (lc) of apical cavity. Lateral crest extending on the distal fourth of the cephalic surface to end in two conical, stout, acute spines (lsp), separated by a wide V-shaped notch, larger cephalically and the smaller laterally oriented; caudal portion of lateral crest with hook-shaped apical notch (an). Mesial spinulose distal lobe, partially visible. In cephalic view (Fig. 2c), gonopod strong, principal axis with proximal half slightly widening towards the base, with elongate vertical groove (vgr), moderately deep and with parallel margins; distal half broadened by the subapical lateral expansion (lex) widened curved (lateral lobe of Rodriguez, 1982). Mesial distal lobe armed with sharp spines, terminated in acute form and with somewhat larger spines. Lateral crest (lc) of the apical cavity smooth, high, wide, rounded and extending on cephalic surface to end in conical spine, acute and strong, lying between subdistal spine of mesial surface and conical lateral spine, slightly curved proximally. Vertical oval gap between mesial lobe and subdistal three spines, slender and coarsely ovoid, evidently separating lateral and mesial apical surfaces of gonopod, continuing distally to form internal borders of apical cavity. Latero-distal shoulder partially visible. In caudal view (Fig. 2d), distal third slightly inclined mesially. Marginal plate (mpl) straight proximally, without row of proximal setae, curved and wider distally; distal mesial angle projected over mesial surface; distal margin concave, forming caudal edge of the apical cavity. Marginal suture arched; lateral suture evident along proximal half of marginal plate, fused with lateral surface along distal half. Subapical lateral expansion broadly curved; disto-lateral shoulder evident. Spinulose distal lobe of mesial surface and subdistal spine triangular, both partially visible. Caudal portion of disto-lateral crest high, with broad, rounded border. Apical cavity (ac) irregular, roughly oval-shaped, oriented caudo-cephalically, with spinules on internal surface of lateral crest; mesial crest rounded; cephalically, inner surface of mesial spinulose lobe above lateral crest; latero-caudal portion continued as apical notch of lateral crest.

***Lobithelphusa mexicana* Rodriguez, 1982**

(Figs. 1, 2)

Lobithelphusa mexicana Rodriguez, 1982: 97, figs. 62, 63.—Villalobos-Figueroa, 1982: 220.—Villalobos-Hiriart *et al.* 1993: 283.—Álvarez *et al.* 1999: 23.—Ng *et al.*, 2008: 175 (in list).—Villalobos-Hiriart & Álvarez, 2008: 248, 296 (in list).—Álvarez & Villalobos, 2016: 253.

Material examined. Holotype, male, cl 42.8 mm, cw 71.2 mm; Playa Vicente (17°37'16.4" N, 92°28'21.6" W; 133 m asl), municipality of Playa Vicente, Veracruz, Mexico, purchase of R. Cuming, NHMUK 1860.23.

Description. In dorsal view (Fig. 1a), carapace transversally oval, widest anteriorly dorsal surface flat, smooth regions faintly indicated, gastric and branchial regions inflated, separated by wide, slightly curved, moderately deep cervical groove, narrowing near anterolateral margin of carapace, reaching it as thin fissure. Frontal region punctate, depressed with respect to carapace surface. Postfrontal lobes distinct, anteriorly marked by depressions, separated by narrow median groove, anteriorly forming V-shaped notch dividing straight superior frontal margin, fading posteriorly. Pair of gastric pits distinct, transversal, angled, close to each other on metagastric region. Lateral margins of carapace serrated, anterior half with sharp granules, posterior half smooth and entire; portion between external orbital tooth and cervical groove straight with low, rounded granules, and in a lower level as rest of the margin. Posterior margin of carapace straight. In frontal view (Fig. 1b), front vertically deflexed and smooth; inferior frontal border granulated, more advanced than the superior border, with narrow medial notch; superior frontal border bilobed, lobes defined by a row of granules, separated by median notch, slightly inclined towards median groove. Superior margin of orbit formed by granules, continuous with inferior frontal border; lower orbital margin marked by row of granules; exorbital angle projected, narrow, acute; internal border of orbit moderately high; orbital hiatus occupied by basal article of antenna. Median septum that divides antennular fossae thin, visible. Epistomal margin with median triangular tooth, tip acutely rounded, separated from lateral teeth on either side by wide notch with granulate borders. Orifice of efferent branchial channels open, with gap between jugal and lateral angles. Pterygostomial area glabrous, faintly granulated (Fig. 1b–d).

First pereiopods distinctly heterochelous, robust, left cheliped larger than right. Left cheliped with merus subtriangular in cross section; inner and outer borders rounded, granulated; lower surface smooth; upper border armed with alternate small and large triangular spines; upper internal angle as a rounded plate whose edge has low teeth. Carpus surface smooth, superior border armed with row of five conical tubercles, two proximal smaller;

internal angle with prominent conical spine. Palm moderately swollen, smooth. Fingers punctate, slightly curved inward, gaping, tips crossing, bearing triangular sharp teeth on cutting edges; dactyl slender, tip abruptly curved downwards, with longitudinal rows of low, rounded granules on dorsal surface; cutting edge with two large proximal teeth, rest decreasing in size distally. Propodus slightly more robust, punctate, cutting edge with three proximal teeth small, rounded, the following two very strong, markedly swollen externally, rest triangular decreasing in size distally, tip stout, moderately upwards, and rounded (Fig. 1e, f). Right cheliped moderately slender; merus internal surface smooth, superior border tuberculate, inferior one granulated; palm smooth, inferior surface delicately granulated; chela with the fingers curved inwards, closing completely, cutting edges armed with triangular teeth, tips crossing; dactyl with dorsal surface granulated; cutting edge of propodus with alternate large and small sized teeth (Fig. 1a–d).

Ambulatory pereopods normal, decreasing in length posteriorly; ischia and meri smooth; carpi and propodi with rugose surface; dactyli bearing 4 or 5 longitudinal rows of small, sharp, corneous spinules; length variable from equal to longer than propodus (Fig. 1a, d).

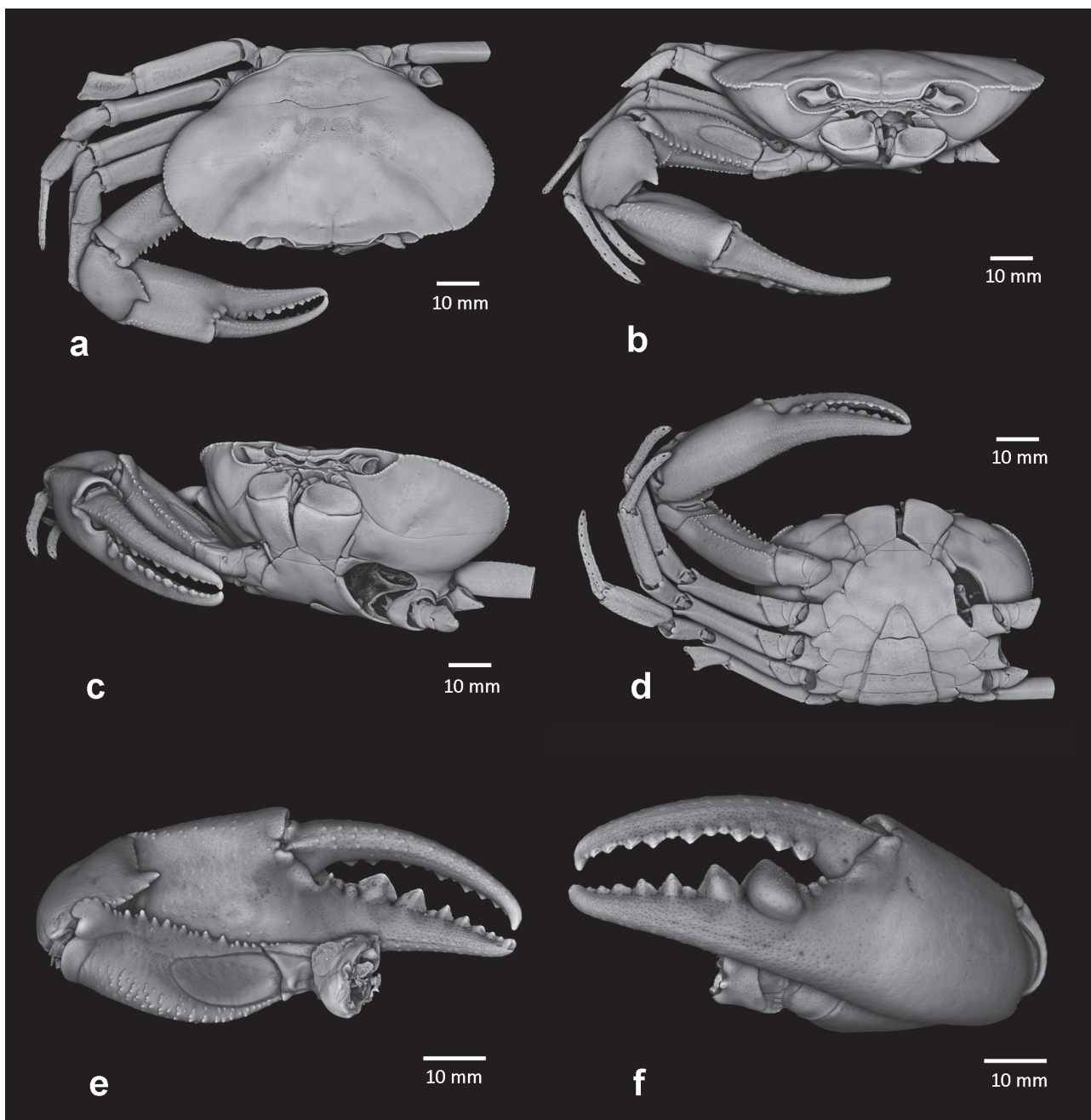


FIGURE 1. *Lobithelphusa mexicana*, male holotype, NHMUK 1860.23. Carapace: dorsal surface, a; frontal portion, b; latero-ventral surface, c; ventral surface, d. Larger chela: internal surface, e; external surface, f.

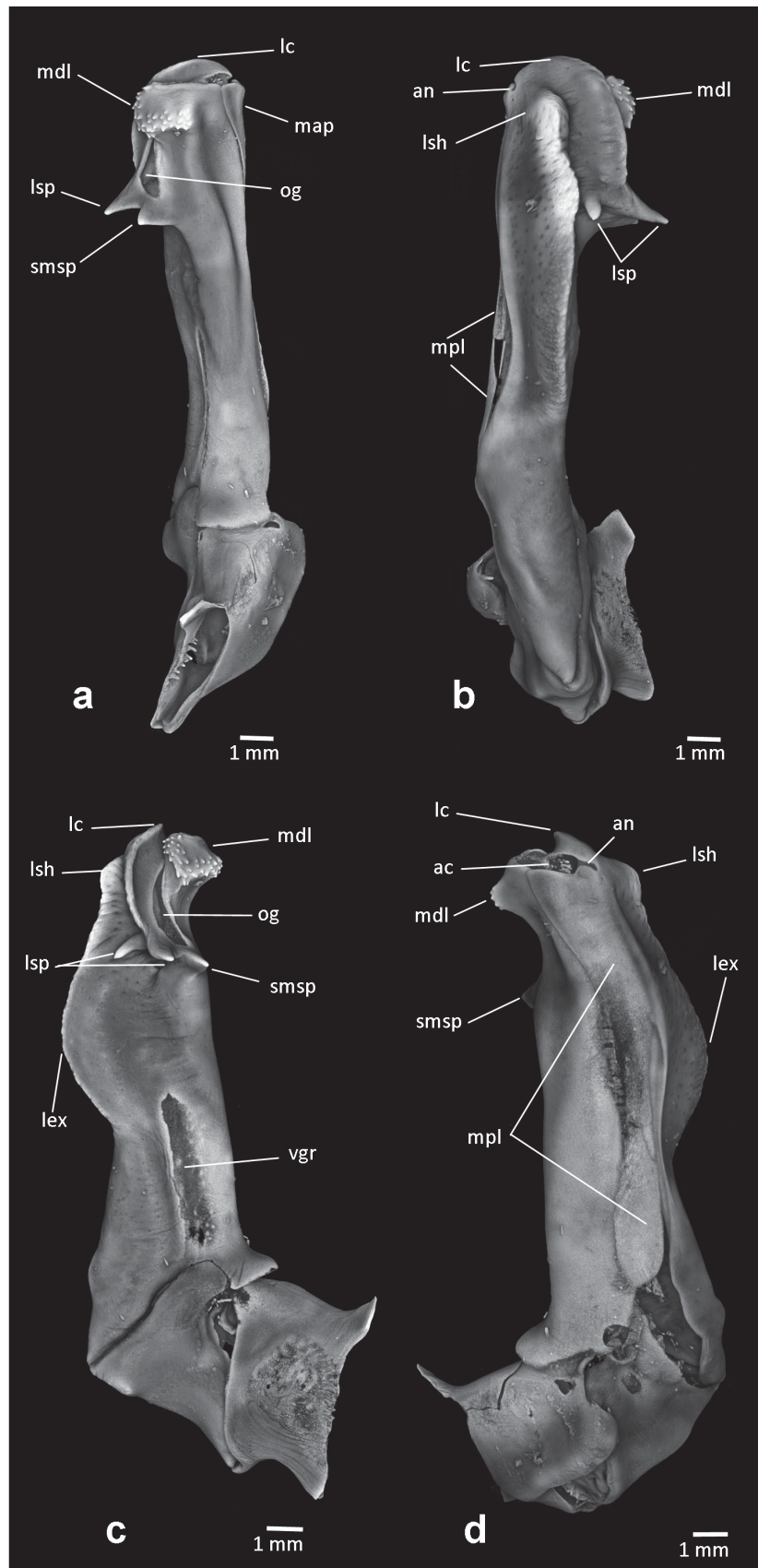


FIGURE 2. *Lobithelphusa mexicana*, male holotype, NHMUK 1860.23. First gonopod, a–d: mesial view, a; lateral view, b; cephalic view, c; caudal view, d. Abbreviations: ac, apical cavity; an, apical notch; lc, lateral crest; lex, lateral expansion; lsp, lateral spines; lsh, lateral shoulder; mdI, mesial distal lobe; mpl, marginal plate; mssp, mesial subdistal spine; og, oval gap; vgr, vertical groove.

TABLE 1. Tribes, genera and species of the subfamily Pseudothelphusinae distributed in Mexico. The classification used follows the proposals of Villalobos-Hiriart & Álvarez (2008); Villalobos & Álvarez (2010); and Ojeda-Escoto (2017).

Tribe Pseudothelphusini Ortmann, 1897	Tribe Potamocarcinini Ortmann, 1897	Tribe Hypobocerini Pretzmann, 1971	<i>Incertae sedis</i>
Genus <i>Disparithelphusa</i> Smalley & Adkison, 1984	Genus <i>Odontothelphusa</i> Rodríguez, 1982	Genus <i>Lobithelphusa</i> Rodríguez, 1982	Genus <i>Ehecatusa</i> Ng & Low, 2010
<i>D. pecki</i> Smalley & Adkison, 1984	<i>O. apicac</i> Villalobos, García & Velázquez, 2009	<i>L. mexicana</i> Rodríguez, 1982	<i>E. chiapensis</i> (Rodríguez & Smalley, 1972)
Genus <i>Ehecatusa</i> Ng & Low, 2010	<i>O. lacandonae</i> Álvarez & Villalobos, 1998	Genus <i>Spirothelphusa</i> Pretzmann, 1965	
<i>E. mixtepecensis</i> (Rodríguez & Smalley, 1972)	<i>O. lacanjae</i> Álvarez & Villalobos, 1998	<i>S. verticalis</i> (Rathbun, 1893)	
Genus <i>Pseudothelphusa</i> de Saussure, 1857	<i>O. maxillipes</i> (Rathbun, 1898)		
<i>P. acahuizotla</i> Ojeda, Villalobos & Álvarez, 2017	<i>O. monodontis</i> Rodríguez & Hobbs, 1989		
<i>P. americana</i> de Saussure, 1857	<i>O. palenquensis</i> Álvarez & Villalobos, 1998		
<i>P. belliana</i> Rathbun, 1898	<i>O. toninae</i> Álvarez & Villalobos, 1991		
<i>P. digneti</i> Rathbun, 1898	Genus <i>Phrygiopilus</i> Smalley, 1970		
<i>P. dilatata</i> Rathbun, 1898	<i>P. monteblancoensis</i> Álvarez & Villalobos, 1998		
<i>P. doentzi</i> Bott, 1968	<i>P. yoshitzi</i> Álvarez & Villalobos, 1998		
<i>P. dugesi</i> Rathbun, 1898	Genus <i>Potamocarcinus</i> H. Milne Edwards, 1853		
<i>P. galloi</i> Álvarez & Villalobos, 1990	<i>P. chajulensis</i> Álvarez & Villalobos, 1998		
<i>P. granatensis</i> Rodríguez & Smalley, 1972	<i>P. hartmanni</i> Pretzmann, 1975		
<i>P. guereroensis</i> Rathbun, 1933	<i>P. magnus</i> (Rathbun, 1895)		
<i>P. hoffmannae</i> Álvarez & Villalobos, 1996	Genus <i>Raddaus</i> Pretzmann, 1965		
<i>P. ixtapan</i> Ojeda, Villalobos & Álvarez, 2017	<i>R. bocourti</i> (A. Milne Edwards, 1866)		
<i>P. jouyi</i> Rathbun, 1893	<i>R. parasilchi mexicanus</i> Pretzmann, 1978		
<i>P. leiophrys</i> Rodríguez & Smalley, 1972	<i>R. tuberculatus</i> (Rathbun, 1897)		
<i>P. lophophallus</i> Rodríguez & Smalley, 1972	Genus <i>Silvathelphusa</i> Villalobos & Álvarez, 2013		
<i>P. mexicana</i> Álvarez, 1987	<i>S. cavernicola</i> Villalobos & Álvarez, 2013		
<i>P. morelosis</i> Pretzmann, 1968	<i>S. kalebi</i> Villalobos & Álvarez, 2013		
<i>P. nayaritae</i> Álvarez & Villalobos, 1994	Genus <i>Typhlopsseudothelphusa</i> Rioja, 1952		
<i>P. nelsoni</i> Rathbun, 1905	<i>T. hyba</i> Rodríguez & Hobbs, 1989		
<i>P. parbelliana</i> Álvarez, 1989	<i>T. mocinoi</i> Rioja 1952		

.....continued on the next page

TABLE 1. (Continued)

<i>P. peytonensis</i> Rodríguez & Smalley, 1972	Genus <i>Tzotzilhelphusa</i> Villalobos & Alvarez, 2013
<i>P. purhepecha</i> Ojeda, Villalobos & Alvarez, 2017	<i>T. villarosalensis</i> Villalobos & Alvarez, 2013
<i>P. rechingeri</i> Pretzmann, 1965	Genus <i>Villalobosius</i> Ng & Low, 2010
<i>P. seiferti</i> Hobbs, 1980	<i>V. leptomelus</i> (Rodríguez & Hobbs, 1989b)
<i>P. sonorensis</i> Miles, 1967	<i>V. lopezformenti</i> (Alvarez & Villalobos, 1991)
<i>P. sulcifrons</i> Rathbun, 1898	Genus <i>Zilchia</i> Pretzmann, 1968
<i>P. terrestris</i> Rathbun, 1893	<i>Z. aspoeckorum</i> (Pretzmann, 1968)
<i>P. zongolicae</i> Alvarez, Villalobos & Moreno, 2012	<i>Z. poglayeneuwalli</i> (Pretzmann, 1978)
Genus <i>Smalleyus</i> Alvarez, 1989	
<i>S. triceristatus</i> Alvarez, 1989	
Genus <i>Tehuana</i> Rodríguez & Smalley, 1972	
<i>T. complanata</i> (Rathbun, 1905)	
<i>T. chontalpaensis</i> Villalobos & Alvarez, 2003	
<i>T. diabolis</i> (Pretzmann, 1978)	
<i>T. jacatepecensis</i> Villalobos & Alvarez, 2003	
<i>T. lamellifrons</i> (Rathbun, 1898)	
<i>T. lamothei</i> Alvarez & Villalobos, 1994	
<i>T. poglayenorium</i> (Pretzmann, 1978)	
<i>T. veracruzana</i> (Rodríguez & Smalley, 1972)	

Ventral surface smooth, sternal sutures discernible; first and second sternites triangular, third to fourth partially fused, fifth to eight well marked (Fig. 1d). Abdomen triangular, all somites free, third somite broadest, sixth longer. Telson triangular, proximal margin slightly sinuous, lateral margins straight, apex rounded (Fig. 1d). Male first gonopod description as in diagnosis of genus.

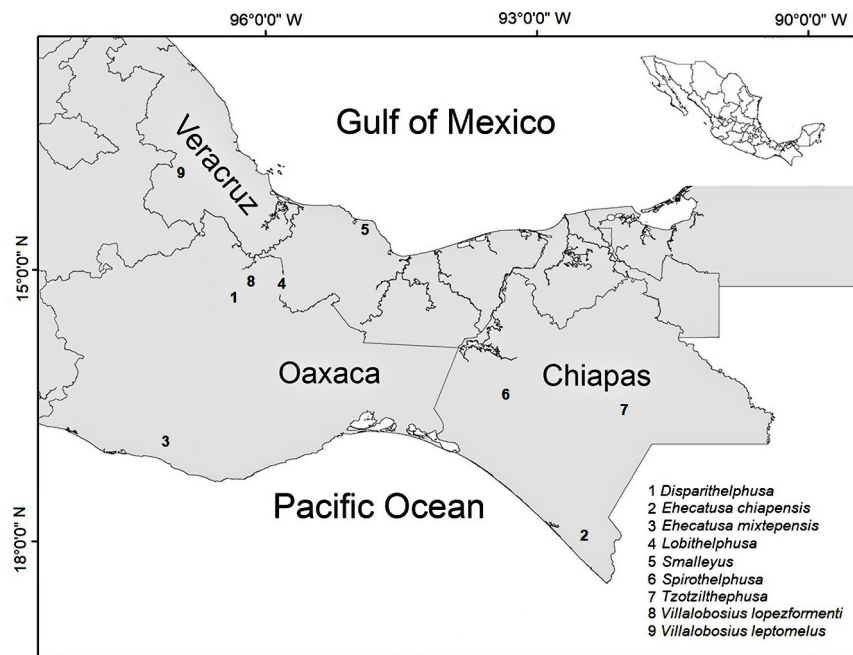


FIGURE 3. Distribution of monotypic and oligotypic genera in southern Mexico. 1. *Disparithelphusa pecki* Smalley & Adkison, 1984, stream 10 km south of Valle Nacional, Oaxaca, Mexico (17°42' N, 96°19' W). 2. *Ehecatusa chiapensis* (Rodríguez & Smalley, 1972), Finca La Victoria (15°11'33.02" N, 92°27'17.66" W), Municipality of Motozintla, Chiapas. 3. *Ehecatusa mixtepecensis* (Rodríguez & Smalley in Smalley, 1970), San Gabriel Mixtepec (16°05'46.15" N, 97°04'53.30" W), Municipality of San Gabriel Mixtepec, Oaxaca. 4. *Lobithelphusa mexicana* Rodríguez, 1982, Playa Vicente (17°37'16.4" N, 92°28'21.6" W), Municipality of Playa Vicente, Veracruz. 5. *Smalleyus tricristatus* Alvarez, 1989, Camino Izquierdo, Sierra of Santa Marta (18°22' 56.47" N, 94°55' 30.40" W), Municipality of Catemaco, Veracruz. 6. *Spirothelphusa verticalis* (Rathbun, 1893), type locality: Tehuantepec, Oaxaca, Mexico (Rathbun, 1893); new locality El Aguacero Cascade (16°45'40.106" N, 93°31'30.24" W), La Venta River, Municipality of Ocozocuahtla, Chiapas. 7. *Tzotzilthelphusa villarosalensis* Villalobos & Alvarez, 2013, deviation road to Sn. Antonio Sujulá (16°21'00.50" N, 92°23'59.70" W), Municipality of Villa de las Rosas, Chiapas. 8. *Villalobosius leptomelus* (Rodríguez & Hobbs, 1989), El Tunel Cave, Mahoilca (= Macuilca, 18°38'49" N, 96°56'58" W), Municipality of Porvenir Zongolica, Veracruz. 9. *Villalobosius lopezformenti* (Alvarez & Villalobos, 1991), El Brujo Cave, Rancho El Guayabo (17° 50' 27.10" N, 96° 11' 38.98" W), 4 km. S of Jacatepec, Municipality of Valle Nacional, Oaxaca.

Discussion

Neotropical freshwater crabs exhibit a remarkable diversity, with a distribution range from northwestern Mexico to approximately the parallel of 12° latitude S in South America including some of the Caribbean islands (Rodríguez & López 2003; Rodríguez & Suárez 2004). Although they have been studied for almost 200 years, more than 50% of them are considered, using the IUCN classification, as Data Deficient and consequently classified by the Red List assessment as priority species for their conservation (Cumberlidge *et al.* 2014; Alvarez & Villalobos 2016).

Five monotypic genera are distributed in Mexico (*Lobithelphusa* Rodríguez, 1982; *Smalleyus* Álvarez, 1989; *Spirothelphusa* Pretzmann, 1965; *Disparithelphusa* Smalley & Adkison, 1984; and *Tzotzilthelphusa* Villalobos & Álvarez, 2013). In addition, *Villalobosius* Ng & Low, 2010, and *Ehecatusa* Ng & Low, 2010, are represented by two species each (Villalobos-Hiriart & Álvarez 2008; Villalobos & Álvarez 2013). All these genera are

characterized by unique G1 morphologies and restricted distributions (Fig. 3), making it difficult to establish their affinities with certainty. With the exception of *Spirothelphusa verticalis* (Rathbun, 1893) and *Disparithelphusa pecki* Smalley & Adkison, 1984, the remaining genera are known from one sample and one male, and have never been collected again. With respect to *L. mexicana*, recent efforts to collect the species at the type locality conducted in March 2018 were unsuccessful. While no specimens of *L. mexicana* could be found, other species of freshwater crabs (*Tehuana* sp. Rodríguez & Smalley, 1972, and *Avotrichodactylus constrictus* (Pearse, 1911)), were common in the area.

Regarding the relationships of *Lobithelphusa*, it was included by Rodríguez (1982) in the Hypolobocerini due to the presence of a lateral “expansion” on the principal axis of the G1. This character was considered homologous to the lateral lobe present in *Hypolobocera* Ortmann, 1897, and other related Colombian and Venezuelan genera (Rodríguez 1982). In *L. mexicana* however, the lateral “expansion” is not as developed as in the South American species and the apical elements are different in shape and position. The Hypolobocerini is the most widely distributed taxon of pseudothelphusid crabs, occurring from southern Mexico to northern South America, in Peru, Ecuador, Panama, Colombia and Venezuela. They show the widest arrange of G1 morphologies, from the typical *Hypolobocera* pattern to the complex forms of *Spirothelphusa* and *Elsalvadoria* Bott, 1967.

A recent study by Poettinger *et al.* (2016) has challenged the monophyly of the Hypolobocerini based on a molecular phylogeny. They suggested that the genera *Achlidon* Smalley, 1964b, *Allacanthos* Smalley, 1964b, and *Ptychophallus* Smalley, 1964b, should form an independent taxon, at the tribe or subfamily level. The division of the Hypolobocerini into several independent taxa seems to be appropriate if the Pseudothelphusidae are to be revised. For the moment, however, the Hypolobocerini, based on the G1 morphology, should include *Hypolobocera* and its allies, *Neostrengeria* Pretzmann, 1965, *Moristchus* Pretzmann, 1965, *Lindacatalina* Pretzmann, 1977, and *Martiana* Rodríguez, 1980.

The redescription of *L. mexicana*, presented here, suggests that this species should not be assigned to the Hypolobocerini or to any other established tribe. If the species is collected again and tissue samples become available, a molecular analysis would serve to elucidate the relationships of this enigmatic taxon.

Finally, the advantage of micro-CT scanning this fragile dry specimen was the clarity of the images that allowed for an accurate redescription of *L. mexicana* without the material having to be sent on loan to Mexico. Consequently, avoiding any more risk of damage to this valuable specimen. Furthermore, the scanned data is now stored and readily available for any future investigations; go to <https://doi.org/10.11646/zootaxa.4586.1.8>.

Acknowledgements

We are grateful to Eric Moreno who prepared the map. We also thank Célio Magalhães and an anonymous reviewer for their helpful comments and suggestions.

References

- Alvarez, F. (1989) *Smalleyus tricristatus*, new genus, new species, and *Pseudothelphusa parabelliana*, new species (Brachyura: Pseudothelphusidae) from Los Tuxtlas, Veracruz, Mexico. *Proceedings of the Biological Society of Washington*, 102 (1), 45–49.
- Alvarez, F. & Villalobos, J.L. (2016) Freshwater decapod diversity and conservation in Mexico. In: Kawai, T. & Cumberlidge, N. (Eds.), *Conservation and Biology of Freshwater Decapoda: A Global Overview*. Springer, Cham, pp. 237–266. https://doi.org/10.1007/978-3-319-42527-6_8
- Alvarez, F., Villalobos J.L., Rojas, Y. & Robles, R. (1999) Listas y comentarios sobre los crustáceos decápodos de Veracruz, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoolología*, 70 (1), 1–27.
- Ball, A.D., Goral, T. & Kamanli, S.A. (2017) Confocal microscopy applied to paleontological specimens. *The Paleontological Society Papers*, 22, 39–55.
- Bott, R. (1967) Fluß-Krabben aus dem wetlichen Mittelamerika (Crust., Decap.). *Senckenbergiana Biologica*, 48 (5/6), 373–380.
- Campos, M.R. (2005) *Freshwater crabs from Colombia. A taxonomic and distributional study*. Academia Colombiana de Ciencias Exactas Físicas y Naturales. Col. Jorge Álvarez Lleras No. 24. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Bogotá, 363 pp.
- Campos, M.R. & Magalhães, C. (2014) *Colombiathelphusa*, a new genus of freshwater crab from Colombia, a new species, and

- the first location record of *Eidocamptophallus chacei* (Pretzmann, 1967) (Crustacea: Decapoda: Pseudothelphusidae). *Zootaxa*, 3860 (6), 571–579.
<https://doi.org/10.11646/zootaxa.3860.6.5>
- Cumberlidge, N., Álvarez, F. & Villalobos, J.L. (2014) Results of the global conservation assessment of the freshwater crabs: The Neotropical region (Brachyura: Pseudothelphusidae and Trichodactylidae), with an update on diversity. *Zookeys*, 457, 133–157.
<https://doi.org/10.3897/zookeys.457.6598>
- Kamanli, S.A., Kihara, T.C., Ball, A.D., Morritt, D. & Clark, P.F. (2017) A 3D imaging and visualization workflow, using confocal microscopy and advanced image processing for brachyuran crab larvae. *Journal of Microscopy*, 266 (3), 307–323.
<https://doi.org/10.1111/jmi.12540>
- Koch, M., Kamanli, S.A., Crimmen, O., Lin, C.W., Clark, P.F. & Āuriš, Z. (2017) The identity of *Monomia argentata* (Crustacea: Brachyura: Portunidae) resolved by X-ray, computed tomography scanning and molecular comparisons. *Invertebrate Systematics*, 31, 797–811.
<https://doi.org/10.1071/IS16058>
- Limaye, A. (2012) Drishti: a volume exploration and presentation tool. In: Stock, S.R. (Ed.), *Developments in X-Ray Tomography VIII. Proceedings of SPIE Vol. 8506 SPIE*. Bellingham, Washington, pp. 1–9.
- Ng, P.K.L. & Low, M.E.Y. (2010) On the generic nomenclature of nine brachyuran names, with four replacement names and two *nomina protecta* (Crustacea: Decapoda). *Zootaxa*, 2489 (1), 34–46.
<https://doi.org/10.11646/zootaxa.2489.1.2>
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, 17 (Supplement), 1–286.
- Ojeda-Escoto, J.C. (2017) *Sistémática y biogeografía de los cangrejos de agua dulce de México de la familia Pseudothelphusidae (Crustacea: Decapoda)*. Ph.D. Dissertation, Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, 124 pp.
- Ojeda-Escoto, J.C., Villalobos, J.L. & Alvarez, F. (2017) Three new species of freshwater crabs of the genus *Pseudothelphusa* (De Saussure, 1857) (Crustacea: Decapoda: Pseudothelphusidae) from Mexico. *Zootaxa*, 4216 (6), 559–571.
<https://doi.org/10.11646/zootaxa.4216.6.3>
- Ortmann, A. (1893) Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VII. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. *Zoologische Jahrbücher Abtheilung für Systematik, Geographie und Biologie der Thiere*, 7, 411–495.
- Ortmann, A. (1897) Carcinologische Studien. *Zoologische Jahrbücher Abtheilung für Systematik, Geographie und Biologie der Thiere*, 10, 258–372.
- Pearse, A.S. (1911) Report on the Crustacea collected by the University of Michigan. Walker expedition in the state of Vera Cruz, Mexico. *Reports of the Michigan Academy Science*, 13, 108–112.
- Poettinger, T.S., Klaus, S. & Schubart, C.D. (2016) Phylogenetic relationships among Neotropical freshwater crabs of the Pseudothelphusidae (Decapoda, Brachyura) and the taxonomic position of *Ptychophallus* and related genera. *Crustaceana*, 89 (14), 1717–1728.
<https://doi.org/10.1163/15685403-00003627>
- Pretzmann, G. (1965) Vorläufiger Bericht über die Familie Pseudothelphusidae. *Anzeiger der Mathematisch-Naturwissenschaftlichen Klasse der Österreichische Akademie der Wissenschaften*, 1965 (1), 1–10.
- Pretzmann, G. (1971) Fortschritte in der Klassifizierung der Pseudothelphusidae. *Aus den Sitzungsberichten der Österreichische Akademie der Wissenschaften*, 179 (8), 15–24.
- Pretzmann, G. (1972) Die Pseudothelphusidae (Crustacea Brachyura). *Zoologica, Stuttgart*, 42 (120), 1–182.
- Pretzmann, G. (1977) Zur Taxonomie, Chorologie und Systematik der mittelländischen Hypolobocerini. *Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Mathematisch Naturwissenschaftliche Klasse*, Abt. 1 (186), 429–439.
- Rathbun, M.J. (1893) Descriptions of new species of American freshwater crabs. *Proceedings of the United States National Museum*, 16 (959), 649–661.
<https://doi.org/10.5479/si.00963801.16-959.649>
- Rodríguez, G. (1980) Description préliminaire de quelques espèces et genres nouveaux de crabes d'eau douce de l'Amérique tropicale (Crustacea, Decapoda, Pseudothelphusidae). *Bulletin du Muséum nationale d'Histoire naturelle, Paris*, 4^e Série, 2, Section A (3), 889–894.
- Rodríguez, G. (1982) Les crabes d'eau douce d'Amérique: Famille des Pseudothelphusidae. *Faune Tropicale*, 12, 1–225.
- Rodríguez, G. & López, B. (2003) Insular species of Neotropical freshwater crabs (Crustacea: Brachyura). *Journal of Natural History*, 37, 2599–2614.
<https://doi.org/10.1080/00222930210155710>
- Rodríguez, G. & Smalley, A. (1972) Los cangrejos de agua dulce de México de la familia Pseudothelphusidae (Crustacea, Brachyura). *Anales del Instituto de Biología Universidad Nacional Autónoma de México*, 40 (1), 69–112.
- Rodríguez, G. & Suárez, H. (2004) A revision of the freshwater crabs of the family Pseudothelphusidae (Decapoda: Brachyura)

- from Peru with notes on the southern limits of the family. *Amazoniana*, 18 (1/2), 11–28.
- Smalley, A. (1964a) A terminology for the gonopods of the American river crabs. *Systematic Zoology*, 13 (1), 28–31.
- Smalley, A. (1964b) The river crabs of Costa Rica, and the subfamilies of the Pseudothelphusidae. *Tulane Studies in Zoology*, 12 (6), 5–13.
- Smalley, A. (1970) A new genus of freshwater crabs from Guatemala, with a key to the Middle American genera (Crustacea, Decapoda, Pseudothelphusidae). *American Midland Naturalist*, 83 (1), 96–106.
- Smalley, A. & Adkison, D.L. (1984) *Disparithelphusa pecki*, a new genus and species of fresh-water crab from Mexico (Brachyura: Pseudothelphusidae). *Journal of Crustacean Biology*, 4 (1), 127–133.
<https://doi.org/10.2307/1547901>
- Villalobos, J.L. & Alvarez, F. (2010) Phylogenetic analysis of the Mexican freshwater crabs of the tribe Pseudothelphusini (Decapoda, Brachyura, Pseudothelphusidae). *Zoological Journal of the Linnean Society*, 160, 457–481.
<https://doi.org/10.1111/j.1096-3642.2009.00606.x>
- Villalobos, J.L. & Álvarez, F. (2013) Two new genera and three new species of freshwater crabs (Crustacea: Pseudothelphusidae: Potamocarcinini) from Chiapas, Mexico. *Zootaxa*, 3599 (5), 457–470.
<https://doi.org/10.11646/zootaxa.3599.5.3>
- Villalobos-Figueroa, A. (1982) Decapoda. In: Hulbert, S.H. & Villalobos-Figueroa, A. (Eds.), *Aquatic biota of Mexico, Central America and the West Indies*. San Diego State University, San Diego, California, pp. 215–238.
- Villalobos-Hiriart, J.L. (2005) *Sistemática de los cangrejos de agua dulce de México, tribu Pseudothelphusini Ortmann, 1897 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae)*. *Análisis filogenético, biogeográfico y descripción de especies nuevas*. Ph.D. Dissertation, Facultad de Ciencias, Universidad Nacional Autónoma de México, 394 pp.
- Villalobos-Hiriart, J.L., Cantú Díaz-Barriga A. & Lira- Fernández, E. (1993) Los crustáceos de agua dulce de México. *Revista de la Sociedad Mexicana de Historia Natural*, Volumen Especial, XLIV, 267–290.
- Villalobos-Hiriart, J.L. & Álvarez, F. (2008) Los cangrejos de agua dulce de la familia Pseudothelphusidae (Decapoda: Brachyura: Eubrachyura) de México. Con un apéndice de las especies citadas para América hasta el 2006. In: Alvarez, F. & Rodríguez, G. (Eds.), *Crustáceos de México: Estado actual de su conocimiento*. UANL-PROMEP-SEP. Dirección General de Publicaciones, Universidad Autónoma de Nuevo León, México, D.F., pp. 239–299.
- Yeo, D.C.J., Ng, P.K.L., Cumberlidge, N., Magalhães, C., Daniels, S.R. & Campos, M.R. (2008). Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. *Hydrobiologia*, 595, 275–286.
<https://doi.org/10.1007/s10750-007-9023-3>